

# Predator-Induced Behavioral and Morphological Plasticity in the Tropical Marine Gastropod *Strombus gigas*

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**Abstract.** Florida queen conch stocks once supported a significant fishery, but overfishing prompted the state of Florida to institute a harvest moratorium in 1985. Despite the closure of the fishery, the queen conch population has been slow to recover. One method used in the efforts to restore the Florida conch population has been to release hatchery-reared juvenile conch into the wild; however, sub-optimal predator avoidance responses and lighter shell weights relative to their wild counterparts have been implicated in the high mortality rates of released hatchery juveniles. We conducted a series of experiments in which hatchery-reared juvenile conch were exposed to a predator, the spiny lobster (*Panulirus argus*), to determine whether they could develop behavioral and morphological characteristics that would improve survival. Experiments were conducted in tanks with a calcareous sand substrate to simulate a natural environment. Conditioned conch were exposed to caged lobsters while conch in the control tanks were exposed to empty cages. Conditioned conch moved significantly less and buried themselves more frequently than the naive control conch. Morphometric data indicated that the conditioned conch grew at a significantly slower rate than the naive conch, but the shell weights of the two groups were not significantly different. This implies that the conditioned conch had thicker or denser shells than the control group. As a result, the conditioned conch had significantly higher survival than naive conch in a subsequent predation

experiment in which a lobster was allowed to roam free in each tank for 24 hours. In the future, the conditioning protocols documented in this study will be used to increase the survival of hatchery-reared conch in the wild.

## Introduction

A growing body of evidence suggests that predators elicit behavioral and morphological responses in their prey. Predators have been shown to influence burial depth, respiration rates, and filtration in clams (Doering, 1982a, b); feeding in copepods (Bollens and Stearns, 1992) and damselflies (Koperski, 1997); foraging behavior and growth rates in intertidal snails (Yamada *et al.*, 1998); behavior and growth rates in larval frogs (Relyea and Werner, 1999); and byssal attachment strength in blue mussels (Reimer and Tedengren, 1997). Additionally, morphological plasticity has been predator-induced in a wide variety of taxa from protozoans to crustaceans (Havel, 1987; Appleton and Palmer, 1988; Adler and Harvell, 1990; Spitze, 1992; Reimer and Tedengren, 1996; Arnqvist and Johansson, 1998; Yamada *et al.*, 1998). In many cases, these responses result in increased fitness or survival of the prey organism (Doering, 1982a; Adler and Harvell, 1990; Reimer and Tedengren, 1996; Yamada *et al.*, 1998).

The queen conch (*Strombus gigas*) is a tropical marine gastropod common to shallow-water seagrass habitats throughout the Caribbean bio-province. Queen conch populations have supported a substantial commercial fishery in the region; however, overfishing has depleted stocks to the point that the species has been included in the Convention on the International Trade in Threatened and Endangered Flora and Fauna (CITES) Appendix II (Bräutigam, 1992). In Florida, a moratorium on harvest was instituted in 1985,

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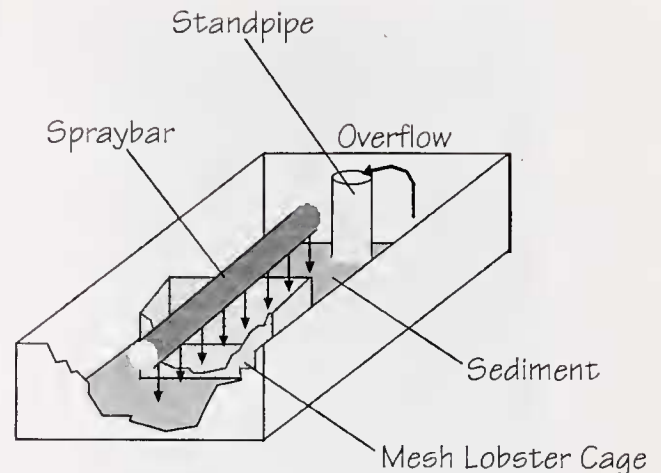
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but conch stocks have not recovered. This has caused many investigators to propose releasing hatchery-reared juvenile conch as a strategy to replenish impoverished stocks (see Stoner, 1997, and Stoner and Glazer, 1998, for reviews). The hatchery's role is to (1) establish or re-establish populations, and (2) supplement or enhance natural production through the release and survival of hatchery-reared juveniles. To accomplish these goals, a successful stock-enhancement program requires a hatchery that can produce not just large quantities of juveniles, but large quantities of high-quality juveniles. Furthermore, after release, these "outplants" must survive and grow to reproduce. Unfortunately, behavioral and morphological deficits have been associated with the husbandry process in queen conch (see Stoner, 1997, and Stoner and Glazer, 1998, for reviews). For example, conch have evolved predator avoidance strategies that include an infaunal early life-history stage (Iversen *et al.*, 1986); however, researchers have observed that released hatchery-reared juvenile conch have lower burial rates than their wild counterparts. Ultimately, this has resulted in higher mortalities in the hatchery cohort (Appeldoorn and Ballantine, 1983; Coulston *et al.*, 1989; Stoner and Davis, 1994). Additionally, the decreased shell weight and shorter apical spines of hatchery-reared *S. gigas* were implicated in their higher mortality relative to wild conch (Stoner and Davis, 1994). To overcome these disadvantages, optimal culture and release strategies are essential.

The extent to which the behavior and morphology of hatchery-reared queen conch can be manipulated before release to maximize survival after release is unknown. However, the survival benefits of exposing laboratory-reared animals to a predator prior to their release have been demonstrated in studies with salmon (Olla *et al.*, 1998) and flounder (Kellison *et al.*, 2000). The present study was initiated to investigate predator-mediated behavioral and morphological plasticity and to determine if any observed phenotypic variations will affect queen conch survival.

### Materials and Methods

We conducted two laboratory experiments to determine the behavioral and morphological effects on queen conch after exposure to one of their main predators, *Panulirus argus*, a species of spiny lobster. We used lobsters 60–80 mm in carapace length for the experiments. Each experiment consisted of two treatments: a conditioned group exposed to a lobster in a cage and a naive control group exposed to an empty cage. Each treatment consisted of three replicates (*i.e.*, tanks) of 20 conch each. Conch were randomly assigned to each tank, and tanks were randomly assigned to each treatment. The first experiment examined differences in burial rates, movement, and shell morphology between the treatments. The second experiment examined the differences in predator-avoidance and conch survival



**Figure 1.** Cut-away view of one of the tanks used to condition queen conch. Tank dimensions were 182 cm long  $\times$  51 cm wide  $\times$  27 cm deep. The lobster was placed in the center of the tank in a mesh cage that allowed water to flow through it. Water entered the tank *via* the spraybar and exited through the standpipe. The sediment was supported off the bottom of the tank by a plastic grid and screen. Drawing not to scale.

between the conditioned and naive treatments after a lobster had been allowed to roam free in the tank.

We conducted all the experiments at the Florida Fish and Wildlife Conservation Commission's (FWC) queen conch hatchery at the Keys Marine Laboratory on Long Key in the Florida Keys. All conch used in the experiments were cultured from egg masses collected in the wild. We used well-described husbandry techniques (see Davis, 1994, for review). The experiments were conducted in six fiberglass tanks with a centralized, flow-through water system (Fig. 1). Each tank had substrate 4 cm to 5 cm deep, consisting of calcareous sand collected from locations that supported wild populations of conch. Before use, the sand was disinfected with dilute chlorine and rinsed with fresh water. The sand was then rinsed with salt water and placed on 1.8-mm mesh supported by a plastic grid about 2 cm off the bottom of the tank. The water circulation and plastic grid minimized the anoxic effects commonly associated with substrate placed directly on the tank bottom.

#### Experiment 1: Conditioning

From a pool of about 300 individuals, 120 conch ranging in size from 35 mm to 40 mm were randomly selected for inclusion in this study. Each day, we fed the conch a diet consisting of a commercially available koi feed (Mazuri Koi Platinum, Purina Feeds, St. Louis, MO), ground and supplemented with 15% oyster shell by dry weight. A uniquely numbered tag was secured to the spire of each conch with Monel wire (Fig. 2), which allowed us to track individuals throughout the duration of the experiments. We measured



**Figure 2.** Juvenile queen conch showing the numbered tag used to distinguish individuals. The tag was attached to the spire of the conch by Monet stainless-steel wire. The shell length (SL) is defined as the linear distance between the tip of the spire and the end of the siphonal canal.

the shell length of each conch to 0.1 mm (Fig. 2) at the onset and completion of the experiments.

Conditioning was initiated by placing a spiny lobster confined within a plastic mesh cage into the tanks. The cage effectively isolated the lobster from the conch while permitting water exchange and visual contact between the two (Fig. 1). Additional juvenile conch similar in size to those in the tank were supplied as food to the predator, thus permitting any chemical alarm substance produced by the feed conch to contact the juveniles being conditioned. Depending on the treatment, juvenile conch were exposed to either a caged predator or an empty cage for 6 h each day (1100 to 1700 hours) for 2 weeks. At 1700, the caged lobsters and empty cages were removed from all tanks.

To facilitate the calculation of conch movements, a quadrat subdivided into  $37 \times 11$  blocks (roughly 5 cm  $\times$  5 cm) was placed on top of each tank. At the initiation of the experiments, we distributed the conch in each tank uniformly, using this Cartesian coordinate grid system. Conch in all tanks were redistributed every morning after their positions were noted. This permitted daily movement information to be unbiased by the final location from the previous day.

We recorded the number of completely buried conch and the position of all individuals at 2-h intervals beginning at 0900 and ending at 1900 hours. These data were used to

assess predator avoidance responses (*i.e.*, burial and mean daily movement) and optimal conditioning time as a function of temporal exposure (*i.e.*, days). A two-way repeated measures ANOVA was used to test for differences in the proportion of buried conch between the two treatments (independent factor) over the duration of the experiment (14 conditioning days = repeated factor). A two-way repeated measures ANOVA of the same design was used to examine the mean daily movement of the individual conch in the two treatments. Planned multiple-comparison *t* tests with a Bonferroni adjustment were used to compare burial and movement between the two treatments for each day.

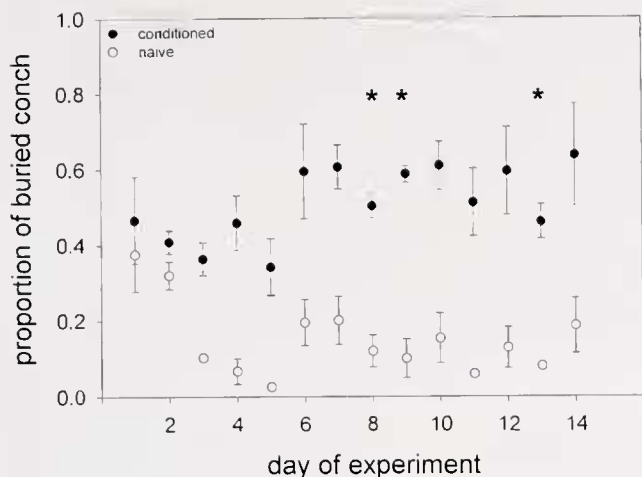
At the end of 2 weeks, the shell length of each individual was recorded for growth calculation. In addition, 10 randomly selected juveniles from each tank were sacrificed. The foot and viscera were removed, and the shell was placed in a drying oven for 24 h at 70 °C; dry shell weight was then recorded. Morphological comparisons (initial shell length, growth, and shell dry weight) of the conch in the two treatments were made using a one-way nested ANOVA (the tanks or replicates were the nested factor).

The conditioning experiment was repeated to determine whether predator-induced morphological changes would arise in a one-week period; however, in this experiment, each treatment (conditioned and naive) contained only two replicates of 20 conch due to the limited inventory of 35-mm to 40-mm conch. No movement or burial data were recorded during this run, but as with the 2-week experiment, growth for all 20 conch and the shell dry weight of 10 randomly selected individuals from each tank were recorded and tested using a one-way nested ANOVA.

The conditioning experiment was repeated once again. This run was designed to test whether predator-induced morphological changes would arise in the presence of lobsters fed on non-molluscan prey (*i.e.*, frozen shrimp). Conditioning lasted 2 weeks. Due to the limited number of animals available, slightly smaller conch (approximately 30 mm) were used than in previous experimental runs, and each treatment (conditioned and naive) contained three replicates of eight conch. No movement or burial data were recorded during this run, but growth for all 24 conch was recorded and tested using a one-way nested ANOVA. We did not examine shell dry weight.

#### *Experiment II: Predator-avoidance and conch survival*

The second experiment was conducted to determine whether any behavioral or morphological differences between the conditioned and naive conch would translate into differences in predation and mortality rates. We used the remaining conch from the one-week conditioning experiment. The conch were left in their respective tanks (two treatments with two replicates, each replicate containing 10



**Figure 3.** The proportion of buried conditioned and buried naive queen conch over the duration of the 2-week conditioning experiment. Error bars represent one standard error. A two-way repeated measures ANOVA showed that conditioned conch buried at significantly higher rate than naive conch ( $P = 0.002$ ) and that there was a significant difference in burial among the days of the experiment ( $P = 0.003$ ). An asterisk indicates that the Bonferroni adjusted planned comparison  $t$  test between the two treatments was significant for that day.

conch), and one lobster was allowed to forage throughout each tank for 24 h.

At the end of the 24 h, the numbers of dead conch, live conch with damaged shells, and live conch with undamaged shells were counted. Those categories were used to assess survival and predator-avoidance as a function of conditioning. Fisher's exact test was used to examine the differences between the two treatments. We compared the number of dead conch to the number of live conch (damaged and undamaged combined) to examine differences in survival between treatments. The numbers of dead conch and live conch with damaged shells were compared against the number of live conch with undamaged shells to examine avoidance through burial. We assumed that conch with undamaged shells escaped detection by burying themselves, although it is possible that the lobsters detected and handled these conch, but did not damage them.

## Results

### Conditioning: Burial and movement

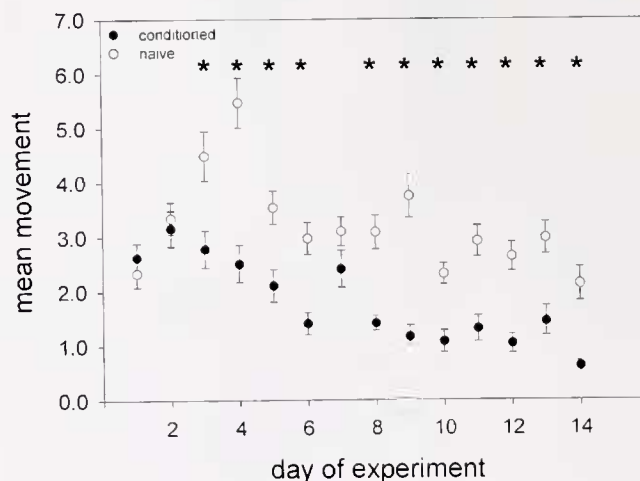
There was a significant difference in the proportion of buried conch between the two treatments and among the days of the 2-week conditioning experiment (repeated measures ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 55.1$ ,  $P = 0.002$ ;  $F_{\text{among days [13, 52]}} = 2.92$ ,  $P = 0.003$ ). The proportion of buried conch in the conditioned treatment increased dramatically on day 6 of the experiment and remained relatively constant afterwards (Fig. 3). Meanwhile, the proportion of buried conch in the naive treatment was fairly steady

throughout the conditioning experiment (Fig. 3). The Bonferroni adjusted multiple comparison  $t$  tests showed that the proportion of buried conch in the conditioned treatment was significantly higher on days 8, 9, and 13 only, although burial diverged after day 3 (Fig. 3).

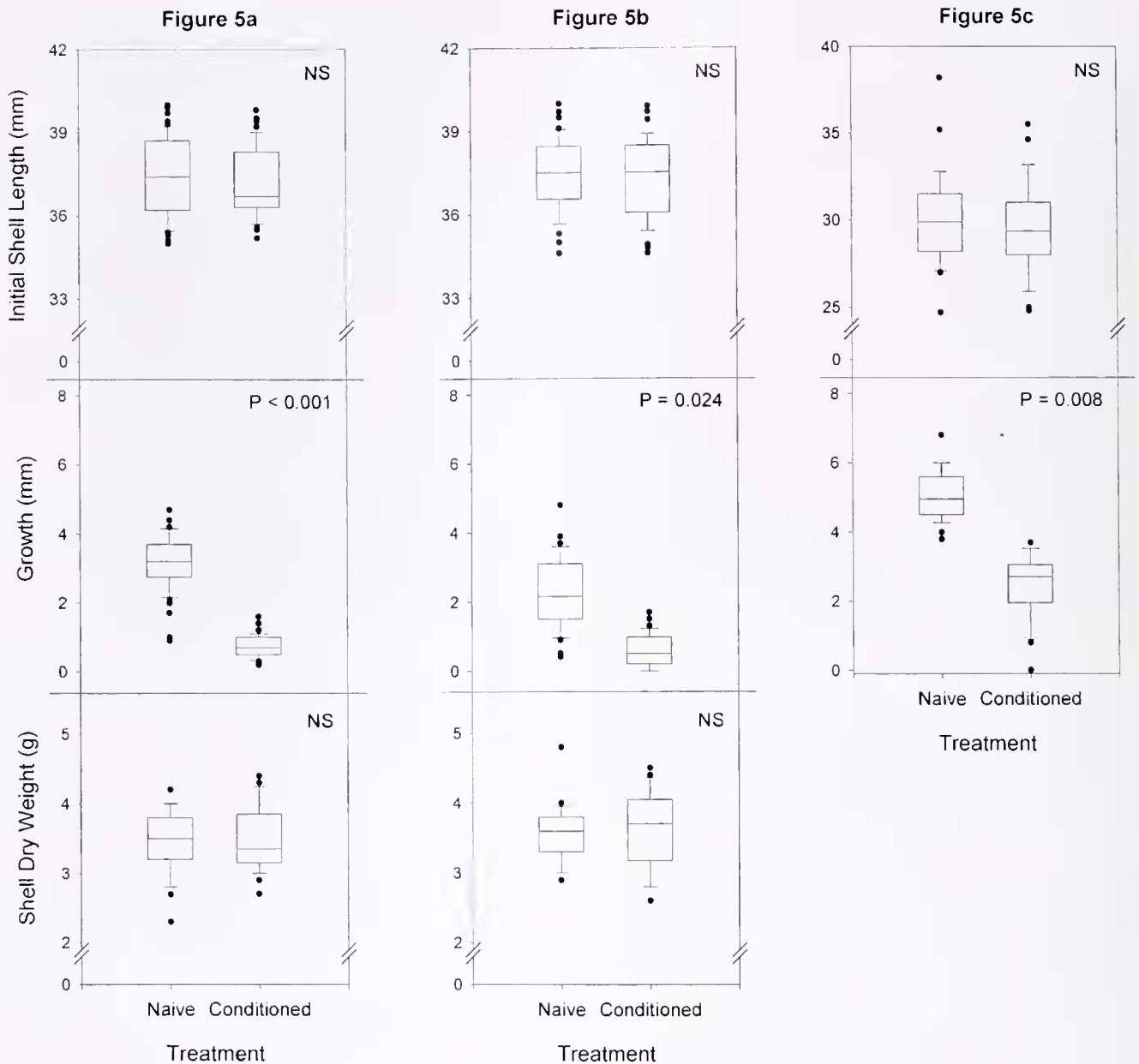
There was a significant difference in the mean movement of conch in the two treatments and among the days of the 2-week conditioning experiment (repeated measures ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 15.1$ ,  $P = 0.018$ ;  $F_{\text{among days [13, 1598]}} = 12.9$ ,  $P < 0.001$ ). The mean movement of the conditioned conch diverged from the naive individuals on day 3 and continued to decrease throughout the rest of the experiment (Fig. 4). The Bonferroni adjusted multiple comparison  $t$  tests showed that the conditioned conch moved significantly less than the naive conch on days 3 through 6 and days 8 through 14 (Fig. 4).

### Conditioning: Morphology

There was no significant difference in initial shell length among the conch chosen for the conditioning experiment (Nested ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 0.536$ ,  $P = 0.505$ ) (Fig. 5a). At the end of 2 weeks, the conditioned conch had grown significantly less than the control group (Nested ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 295$ ,  $P < 0.001$ ), but the shell weights of the two groups were not significantly different (Nested ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 0.128$ ,  $P = 0.738$ ) (Fig. 5a). None of the nested factors (*i.e.*, the tanks) within these ANOVAs were significantly different (initial shell length:  $F_{\text{among replicates [4, 112]}} = 1.11$ ,  $P = 0.354$ ;



**Figure 4.** The mean movement of conditioned and naive queen conch over the duration of the 2-week conditioning experiment. Error bars represent one standard error. A two-way repeated measures ANOVA showed that conditioned conch moved significantly less than naive conch ( $P = 0.018$ ) and that there was a significant difference in movement among the days of the experiment ( $P < 0.001$ ). An asterisk indicates that the Bonferroni adjusted planned comparison  $t$  test between the two treatments was significant for that day.



**Figure 5.** Initial shell length, growth, and shell dry weight of naive and conditioned queen conch in the 2-week conditioning experiment (5a), the 1-week conditioning experiment (5b), and the 2-week conditioning experiment in which the lobsters were fed non-molluscan prey (*i.e.*, frozen shrimp) (5c). Shell dry weight was not examined in the third experiment (5c). The boxes represent the interquartile ranges, which contain 50% of the values. The line bisecting the box represents the median. The whiskers extend to the 90th percentile. Dots represent outliers. When significant,  $P$  values from the nested ANOVAs are given in the upper right-hand corner of each graph; NS indicates that the test was not significant.

growth:  $F_{\text{among replicates [4, 112]}} = 1.56$ ,  $P = 0.191$ ; shell weight:  $F_{\text{among replicates [4, 52]}} = 0.270$ ,  $P = 0.896$ ). Two conch in the conditioned treatment were not included in these analyses because they buried themselves under the sand and the plastic grid, and were not found until the experiment was disassembled.

The conditioning experiment was repeated to determine whether these predator-induced morphological changes would arise in a one-week period. Again, there was no significant difference in initial shell length among the conch chosen for the two predator treatments (Nested ANOVA:  $F_{\text{btwn treatments [1, 2]}} = 0.360$ ,  $P = 0.609$ ) (Fig. 5b). After one

week, the conditioned conch had grown significantly less than the control group (Nested ANOVA:  $F_{\text{btwn treatments [1, 2]}} = 40.7$ ,  $P = 0.024$ ), and again, the shell weights of the two groups were not significantly different (Nested ANOVA:  $F_{\text{btwn treatments [1, 2]}} = 0.013$ ,  $P = 0.921$ ) (Fig. 5b). None of the nested factors within the ANOVAs were significantly different (initial shell length:  $F_{\text{among replicates [2, 75]}} = 0.832$ ,  $P = 0.439$ ; growth:  $F_{\text{among replicates [2, 75]}} = 1.96$ ,  $P = 0.149$ ; shell weight:  $F_{\text{among replicates [2, 35]}} = 2.59$ ,  $P = 0.090$ ). One juvenile in the conditioned treatment was not included in these analyses because it buried itself under the sand and the plastic grid, and was not found until the experiment was disassembled.

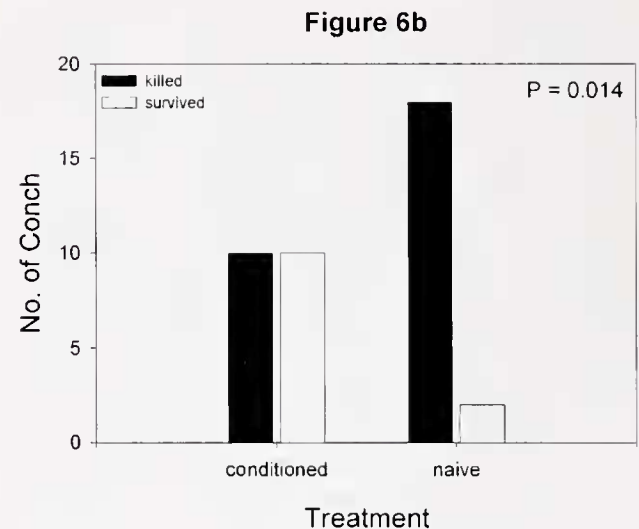
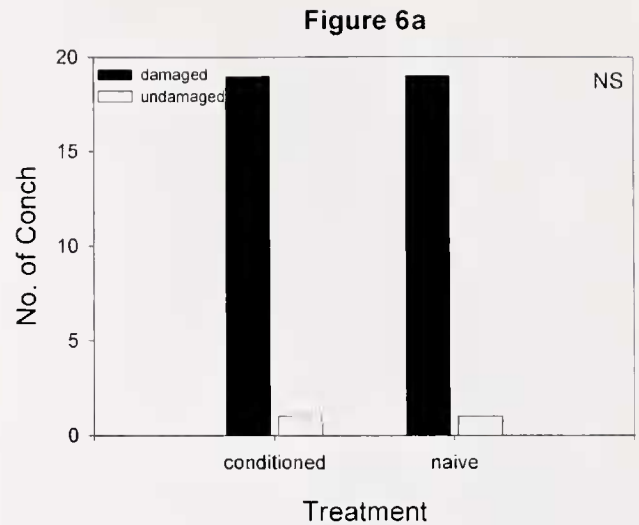
The next run was designed to determine whether predator-induced morphological changes would arise after 2 weeks of conditioning in the presence of lobsters fed on frozen shrimp. There was no significant difference in initial shell length among the conch chosen for the two predator treatments (Nested ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 0.295$ ,  $P = 0.616$ ) (Fig. 5c). The nested factor (*i.e.*, the tanks) within this ANOVA was not significantly different ( $F_{\text{among replicates [4, 42]}} = 0.910$ ,  $P = 0.467$ ). After 2 weeks, the conditioned conch had grown significantly less than the control group (Nested ANOVA:  $F_{\text{btwn treatments [1, 4]}} = 24.7$ ,  $P = 0.008$ ) (Fig. 5c). However, the nested factor within this ANOVA was significantly different ( $F_{\text{among replicates [4, 42]}} = 7.14$ ,  $P < 0.001$ ). The conch in one of the tanks within the conditioning treatment had much less growth ( $1.35 \pm 0.795$  mm) than the other two conditioned tanks ( $3.00 \pm 0.537$  mm and  $2.89 \pm 0.464$  mm). When this tank was removed from the analysis, the conditioned conch still had significantly slower growth.

#### Predator-avoidance and conch survival

Predator-avoidance was independent of conditioning (Fisher's exact test:  $P = 1.0$ ); only two individuals (one from each treatment: conditioned and naive) avoided detection through burial (Fig. 6a). However, survival was dependent on conditioning (Fisher's exact test:  $P = 0.014$ ). Conditioned conch survived their encounter with the lobster 50% of the time, whereas only 10% of the naive conch survived (Fig. 6b).

#### Discussion

Many organisms have been shown to produce adaptive phenotypes in response to environmental changes or stimuli (see Havel, 1987, and Adler and Harvell, 1990, for reviews). In the queen conch, shell morphology is plastic depending on environmental conditions (environmental induction) (Alcolado, 1976; Stoner and Davis, 1994; Martin-Mora *et al.*, 1995). Therefore, by altering the culture environment in the hatchery, it may be possible to induce the expression of different phenotypes (phenotypic plasticity). Predator-me-



**Figure 6.** The number of conditioned and naive queen conch damaged (6a) and killed (6b) during the predator-avoidance and conch survival experiment. We assumed that conch with undamaged shells escaped detection *via* burial. Fisher's exact test showed that predator-avoidance was independent of conditioning (6a,  $P = 1.0$ ); however, conditioned conch had significantly higher survival than their naive counterparts (6b,  $P = 0.014$ ).

diated changes in behavior and morphology have been described for a variety of species, and the present experiments demonstrate that these alterations can be induced in hatchery-raised queen conch as well.

We have shown that conch exposed to a predator for 2 weeks grew significantly slower; but their shell weights were practically identical to naive conch, implying that conditioned animals had thicker or denser shells. These morphological changes in conditioned conch were also induced after exposure to the lobster for just one week. The

aim of the study was not to determine the mechanism of the changes in behavior and morphology, but to determine whether the changes could be predator-induced in queen conch. Nevertheless, the mechanism for the morphological responses may have been visual or mechanical cues from the lobster, odor cues produced by the lobster, a chemical alarm substance excreted by the feed conch, or a combination of these. However, it is unlikely that a species-specific alarm substance was the sole cause of the morphological variability, because conditioned conch exposed to lobster fed on frozen shrimp also had slower growth rates than naive individuals. A study conducted on the intertidal gastropod *Thais lamellosa* produced similar results. *Thais* developed predator-resistant thicker shells when in the presence of crabs fed conspecific snails and in the presence of crabs fed frozen fish (Appleton and Palmer, 1988). Queen conch probably detect predators through their chemosensitive tentacles and use their keen eyesight to orient the escape response correctly, as reported with *Strombus maculatus* (Field, 1977).

The shell's primary function is protection; as a protective structure, the molluscan shell must be able to resist breakage. Spiny lobsters peel shells with their greatly enlarged mandibles by breaking off successive pieces of shell, beginning at the outer lip (Davis, 1992); small conch are especially prone to this type of breakage because of their thin shells. The conditioned conch grew at a slower rate than the control group, yet they had thicker or denser shells. Therefore, exposure to a predator before release will probably improve survival, because juvenile queen conch with thicker or denser shells would be better adapted to resist having their shells crushed or peeled. However, a thicker shell will not necessarily reduce all predation mortality; for example, it will not deter crustaceans and molluscs that attack through the aperture (Ray and Stoner, 1995). Therefore, a conch's ability to detect, recognize, and avoid predators (by burying themselves) is also important in reducing predation mortality.

Glazer and Jones (1997) reported that hatchery-reared juvenile conch incurred significantly higher mortalities during the first week after release. We were able to significantly alter the morphology and behavior of hatchery-raised conch in a week's time. It is apparent from the results of both studies that the first week after release is crucial. Evidently, it takes about one week for outplants to adjust to life in the wild; however, conditioning may be able to reduce this period of adjustment and decrease the level of mortality associated with the first week after release. This is especially likely considering that we have shown that both optimal burial and movement responses are induced after one week of exposure to the lobster (Figs. 3 and 4).

The predator-induced morphological and behavioral differences documented in this study are interrelated, as buried conch have a tendency to move less. It is no coincidence

then that the conditioned conch also had slower growth and thicker or denser shells. In gastropods, shell material is deposited along the aperture in the spiral direction with the mantle lying at the growing edge (Vermeij, 1993). The inner layer of shell is added last, well back from the growing edge and is deposited by the mantle's surface, not the mantle's margin (Vermeij, 1993). When growth in the spiral direction is not occurring, the mantle margin withdraws from the edge, and new shell material is deposited only on the innermost layer (Vermeij, 1993). A conch that is sedentary and buried does not have its mantle at the growing edge but continues to deposit calcium carbonate on the inner layer of the shell, which explains the slower growth and coincidental thicker or denser shells of the conditioned conch. Therefore, by inducing changes in the conch's behavior, their morphology was changed as well.

Other studies have also shown that predator-induced changes in prey behavior affect prey activity and growth. Searching for food increases the risk of predation; therefore, many taxa reduce activity when in the presence of predators (Doering, 1982b; Lima and Dill, 1990; Bollens and Stearns, 1992; Koperski, 1997; Yamada *et al.*, 1998; Relyea and Werner, 1999). These changes in prey behavior are presumed to reduce (1) the rate of predator encounters, (2) the time spent vulnerable to attack, and (3) the probability of death in an encounter (Lima and Dill, 1990). We have demonstrated that by conditioning hatchery-raised conch to one of their principal predators, they can develop behavior and morphology that may accomplish all three survival strategies. Burial will decrease the rate of predator encounters by reducing exposure time, and thicker shells will reduce the probability of mortality if confronted by a shell-peeling or shell-crushing predator.

These predator-induced defense mechanisms were tested in our second experiment (predator-avoidance and conch survival). This experiment showed that the anti-predator morphological changes that took place in conditioned conch were enough to significantly increase their survival over their naive counterparts. A closer inspection of the data showed that most (83.3%) of the conch that survived had incurred some shell damage but escaped being eaten, presumably because their thicker or denser shells were able to resist the shell-peeling lobsters. Davis (1992) reported that hatchery-raised queen conch less than 40 mm in shell length were consumed by lobsters similar in size to those used in this study, whereas larger juvenile conch (>50 mm) suffered damage, but survived. Jory and Iversen (1988) reported that shell strength increased exponentially once conch reached 55 mm in shell length. Therefore, by conditioning juveniles and inducing adaptive morphologies by changing their behavior, the effective size or shell strength of hatchery-reared conch is increased, resulting in survival rates similar to those of larger conch.

The increased burial frequency of the conditioned conch

proved to be ineffective in our predator-avoidance and conch survival experiment; only 16.7% of the conch that survived escaped detection through burial. This predator-avoidance behavior should have allowed more individuals to remain undiscovered. A similar study with the hard clam *Mercenaria mercenaria* showed that the clams burrowed deeper into the sediment when subjected to predacious sea stars, and that this behavior increased survival over individuals that were not allowed to burrow more deeply (Doering, 1982a). The sediment in our tanks may not have been deep enough for the buried conch to avoid detection or the conch density may have been artificially high, allowing the lobster to efficiently forage the entire tank. Deeper sediment or reduced conch densities might have yielded different results.

Stock enhancement through mariculture may be one of the only ways to restore queen conch populations in the Florida Keys. Because of high monetary costs, the usual objective of most conch hatchery operations is to produce the largest product in the quickest time possible. However, this strategy may not be effective in a restoration context. The results of our experiments have shown that the production of fast-growing individuals should not necessarily be the determining factor in the success of a stock-enhancement facility. Rather, it is crucial to release well-adapted individuals in the appropriate habitat to maximize survival. The conditioning protocols documented in this study will be integrated into future releases of hatchery-raised conch to increase outplant survival and increase the cost-effectiveness of our stock rehabilitation program for queen conch.

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